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Creating and *De Novo* Improvement of New Allopolyploid Crops for Future Agriculture

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ABSTRACT

The development of climate change resilient crops is conducive to meeting the increasing threat of supporting the growing world population. Polyploidy occupies an important position in angiosperm evolution, as a key factor that shapes plant biodiversity, growth vigor, environmental adaptation, and emerging chemical compounds. In this review, we outlined the development and application of creating new allopolyploids using sexual and asexual approaches and their potential benefits and problems. We described how polyploidization caused strict genome modification at cytogenetic, genetic, and epigenetic levels with emphasis on the latest update on genome assembly of newly synthesized allopolyploids. Despite the success in creating new allopolyploids in many genera, it occasionally gave rise to undesirable traits to impact the utilization of newly synthetic allopolyploids. Recent developments in the *de novo* domestication of wild species through genome editing provide a route to create new crops to secure the global food supply. Following the strategy, *de novo* improvement of newly synthetic allopolyploids using genome editing could be galvanized to rapidly improve newly synthesized allopolyploids to meet agriculture demands and enable plant breeders to keep pace with global changes.

KEYWORDS

De novo improvement; genome editing; genome stability; newly-synthesized allopolyploid

I. Introduction

The predicted global human population by 2050 is ~10 billion with a 70% increase in food production yield required to keep pace (Springmann *et al.*, 2018). A major challenge is learning how to feed the expanding population. Traditional breeding methods have generated high-yield nutritious crops, particularly due to the Green Revolution and plant breeding advances (Khush, 2001). Recently, new plant breeding techniques including marker-assisted selection, genomic selection, genome editing, and genetic modification are used for crop improvement (Schaart *et al.*, 2016; Wallace *et al.*, 2018; Hickey *et al.*, 2019). However, crop production appears to be stagnating and even declining due to climate change, biodiversity decline, limited availability of arable land, and other issues (Ray *et al.*, 2012). In particular, extreme weather events, such as drought, flood, heat, and catastrophic storm are expected to rise (Cook *et al.*, 2014). Therefore, improving agricultural productivity and sustainability is essential through modifying current crops and developing new crops with a higher yield, richer nutrients, stronger pest- and disease-resistance, and climate intelligence.

The selection of ideal traits for genetic improvement in crop breeding often simulates natural evolution, enabling the survival, prosperity, and reproduction of a species in the wild. Evolutionary history shows the high frequency of ancient and recent polyploidization events among plants, particularly angiosperms (Jiao *et al.*, 2011). Plant diversity and speciation are usually promoted by interspecific hybridization in nature (Ramsey and Schemske, 1998), and many essential crops including common wheat, cotton, and canola are allopolyploids. Allohexaploid common wheat (*Triticum aestivum*, AABBDD) is resulted from hybridization between tetraploid emmer wheat (*T. turgidum*, AABB) and diploid wild goat grass *Aegilops tauschii* (DD) (Marcussen *et al.*, 2014). Repeated polyploidization of *Gossypium* genomes to form tetraploid cotton increases fiber productivity and quality (Paterson *et al.*, 2012). A hypothetical model of multi-vertex reciprocal hybridization in *Brassicaceae* crops gives rise to varied allopolyploid

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species (Cheng *et al.*, 2017). Naturally polyploid plant species usually show modified growth and adaptation to harsh circumstances with evolutionary advantages (McKeown *et al.*, 2013; Soltis *et al.*, 2014; del Pozo and Ramirez-Parra, 2015). Such advantages have been introduced to crop breeding programs (Li *et al.*, 2015; Mason and Batley, 2015; Sattler *et al.*, 2016; Quezada-Martinez *et al.*, 2021).

Crop development may be improved by interspecific hybridization to create new polyploidy species (Mason and Batley, 2015; Sattler *et al.*, 2016). Newly synthesized allopolyploids are challenged by the coordination of different sub-genomes with independent genetic and epigenetic regulatory consequences within a single cell (Comai, 2005). Merging two or more different genomes may induce "genome shock" of genome-wide changes resulting in rapid genomic reshuffling or relative stability (Mcclintock, 1984). The development of molecular genetics and genomic technology has addressed genomic instability and exploited hybrid speciation to create new crop species. Next-generation sequencing technology combined with association analysis and genome editing is able to quickly and efficiently recognize, choose, or even design ideal allelic variation (Li *et al.*, 2015; Mason and Batley, 2015; Quezada-Martinez *et al.*, 2021).

Allopolyploidization, the main source of evolutionary innovation, is the driver for speciation as well as environmental adaptation (Comai, 2005; Leitch and Leitch, 2008). For plants, allopolyploidization significantly improved crop domestication by the extraordinary attributes in numerous modern crop plants conferred by ancient allopolyploidization events (Paterson, 2005). In this review, we introduced approaches for resynthesizing allopolyploids via sexual interspecific hybridization and asexual grafting. We reviewed the latest advancements in understanding the mechanism of genome from cytological, genetic, and epigenetic perspectives. Furthermore, a technological toolbox comprised of an omics-aided assay coupled with genome editing techniques is presented to help create new crop species with desirable traits for future agriculture.

II. Creating new allopolyploids *via* sexual and asexual approaches

Interspecific or intergeneric hybridization followed by chromosome doubling is practical to create new allopolyploids (Figure 1a), which are usually exploited to broaden genetic diversity in many agriculturally important crops (Chen *et al.*, 1997; FitzJohn *et al.*, 2007; Mestiri *et al.*, 2010; Mason and Batley, 2015; Zhang *et al.*, 2022). However, critical challenges remain to produce a genetically diverse allopolyploid pool, as this is a long list (1) species-specific hybridization barriers, (2) low efficiency in chromosome doubling, (3) quick chromosomal elimination from the genomes of parental species, (4) self-incompatibilities, and (5) cross-incompatibilities among germplasm pools (Zhang *et al.*, 2021). Understanding the pivotal factors that influence interspecific cross-compatibility is crucial to allopolyploid development because hybrids can be only created through combinations or along the inherent direction (FitzJohn *et al.*, 2007). For example, embryo rescue is crucial to successful crosses among species, and even within the same species due to cross-compatibility or incompatibility. Determining the genetic mechanism of interspecific incompatibility and compatibility helps raise the number of potential cross combinations and general genetic diversity (Zhang *et al.*, 2021). Spontaneous chromosome doubling of interspecific hybrids varies, depending on the species. Colchicine is often used for chromosome doubling, however, it generally has a low chromosome doubling success rate, possibly causing damage via chromosome rearrangements or other mutations in treated plants (Xu *et al.*, 2007; Zhang *et al.*, 2021). Mitosis-inhibiting herbicides like dinitroanilines pertain to colchicine alternatives (Dhooghe *et al.*, 2011). Taken together, successful transfer of agronomical traits among species is decided by multiple factors, such as similarity of source (wild relative) genomes with target (crop) genomes, the ease in hybrid production, the frequency and distribution of crossovers in interspecific hybrid meiosis, as well as the ease in recovery of introgression lines.

The economically important *Brassica* genus provides a valuable model for the study of resynthesis of new allopolyploids. *Brassica* genomes are thought to have undergone multiple rounds of polyploidization generating multifarious species within this genus (Cheng *et al.*, 2017). It is widely known that three diploid species: *B*rassica *rapa* (AA), *Brassica nigra* (BB), and *Brassica oleracea* (CC) gave rise to three allotetraploid species (*Brassica napus* AACC, *Brassica juncea* AABB, and *Brassica carinata* BBCC) through natural hybridization and allopolyploid speciation events interpreted by the U's triangle model in the *Brassica* genus (UN, 1935). Scientists raised the possibility of creating trigenomic bridges for *Brassica* improvement involving interspecific hybrid plants containing three genomes with different combinations: triploid (ABC), unbalanced tetraploid

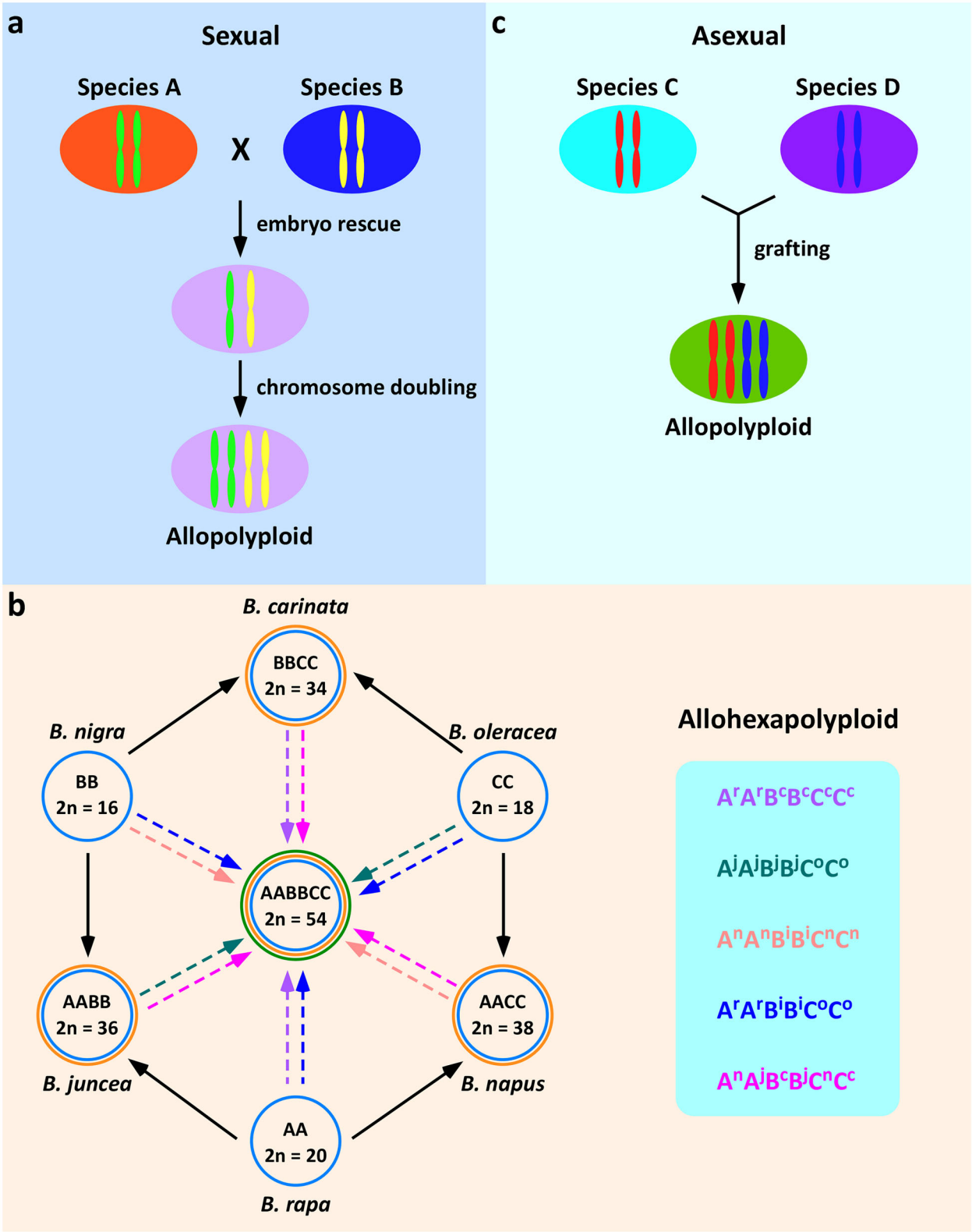

Figure 1. Strategies to resynthesize allopolyploids. (a) Allopolyploids were generated via interspecific or intergeneric sexual hybridization, followed by chromosome doubling wherein embryo rescue is usually used due to hybridization incompatibility. (b) Approaches to produce allohexaploids from the *Brassica* U's triangle species. Possible pathways (dotted arrows) of hybridizations between- or among six evolutionarily established diploids and allotetraploids and possible chromosome components in newly synthesized allohexaploids with the same colors. (c) Allopolyploids were formed via asexual grafting.

(AABC), pentaploid (AABCC), and hexaploid (AABBCC) (Chen *et al.*, 2011). *Brassica* breeders can acquire entire genetic resources from the U triangle to improve the current species and develop novel agricultural species with desirable traits (Zhang *et al.*, 2022). Allohexaploid *Brassica* hybrids have been the target of plant breeding study for years to benefit plant breeding and to deepen awareness about polyploid plant evolution (Gaebelein and Mason, 2018). Some successful cases of new allohexaploids were generated through different interspecific hybridization approaches (Pradhan *et al.*, 2010; Tian *et al.*, 2010; Geng *et al.*, 2013; Gupta *et al.*, 2016; Zhang *et al.*, 2021). New allohexaploid *Brassica* crops have several advantages compared with the current *Brassica* diploid and allotetraploid species through integrating genetic diversity and traits of the six species with additional allelic heterosis in the extra genome (Figure 1b). It is possible to extend the interspecific hybridization between *Brassica* and allied genera within the *Brassicaceae* by exploiting some of the wild relatives exhibiting significant tolerance to biotic and abiotic stress in the hybridization strategy to improve resilience of the newly synthesized crop cultivars (Mason and Batley, 2015; Cheng *et al.*, 2017; Kumari *et al.*, 2020; Quezada-Martinez *et al.*, 2021; Feng *et al.*, 2022). However, this approach requires significant effort since it relies on the hybridization complexity and genetic distance between the source and target, crossover frequencies and distributions in alloploids, and the capacity to choose ideal introgressions when minimizing linkage drag (Quezada-Martinez *et al.*, 2021; Zhang *et al.*, 2021).

In general, allopolyploidization existed in hybridization events of species accompanied by or followed by genome duplication (Hegarty and Hiscock, 2008; Soltis and Soltis, 2009). Natural grafting created a novel allopolyploid plant species using a herbaceous species and a woody species from the nightshade family (Fuentes *et al.*, 2014), indicating whole nuclear genomes are transferred among plant cells and novel species can be asexually produced (Figure 1c). It offers us an approach to produce novel plant species as new crops (Jones, 2014). Future work is required to determine if the process can occur in nature. Horizontal gene transfer, referring to the movement of genetic information among organisms, has become amenable to experimental investigation (Van Etten and Bhattacharya, 2020; Wickell and Li, 2020). Horizontal gene transfer, discovered as the asexual process, generates novel species and novel combinations of nuclear and organellar genomes (Bock, 2017).

III. Omics-aided assay of genetic and epigenetic characteristics of newly synthesized allopolyploids

Primary allopolyploids usually demonstrate high genetic instability that is disadvantageous for crop breeding (Ramsey and Schemske, 2002; Li *et al.*, 2016). Chromosome instability is common in primary allopolyploids from divergent plant taxa (Xiong *et al.*, 2011; Sosnowska *et al.*, 2020; Zhao *et al.*, 2021) and leads to high frequency aneuploidy featuring variations of the copy number of chromosomes wholly or partly relative to the standard karyotype (Zhang *et al.*, 2013a). Chromosome-level perturbation is the first reflection of nascent allopolyploidization (Xiong *et al.*, 2011). Extensive aneuploidy can be found from early and successive generations (95% after 10 self-generations) of resynthesized allotetraploid *Brassica* (Xiong *et al.*, 2011). Whole-chromosome aneuploidy is a common phenomenon of nascent allohexaploid wheats (Zhang *et al.*, 2013b). The attributes of chromosomal changes among phylogenetically different plant taxa suggest gene dosage balance is the main restrictive mechanism of aneuploid retention (Chester *et al.*, 2012). Aneuploidy is probably mitigated through cytological diploidization caused by preferred DNA elimination of one genome over the other, thereby increasing the divergence of homologous chromosomes (Feldman *et al.*, 2012). Besides, aneuploidy exhibits progenitor dependency. For instance, several hybrids demonstrate higher aneuploid frequency and a lower ratio (Mestiri *et al.*, 2010; Zhou *et al.*, 2016). Whereas, fast and wide structural instabilities like DNA elimination serve as the main genetic variations of newly synthesized wheat allotetraploids (Ozkan and Feldman, 2001; Kashkush *et al.*, 2002). Appropriate genome combinations like AABB (or AASS) instead of AADD are key to karyotype stabilization that may contribute to successful speciation, variations of the copy number of coding genes, and localized changes of genomic repeats (Zhang *et al.*, 2013a). The loss of chromosome fragments in merely one sub-genome after homologous exchanges might consist of a mechanism underlying biased genome fractionation of newly synthesized allopolyploids. Preexisting meiosis gene variants of allotetraploid parents possibly contribute to stabilizing meiosis of newly synthesized allohexaploids (Gaebelein *et al.*, 2019).

The genomic interactions among independent subgenomes in a newly synthesized allopolyploid induce wide and quick chromosome rearrangement, and genome-wide transcriptome changes (Gaeta *et al.*, 2007;

Buggs *et al.*, 2011). Transcriptomic analysis indicated a homeolog expression bias and expression level dominance of newly synthesized allopolyploids (Yoo *et al.*, 2013; Wang *et al.*, 2016; Yang *et al.*, 2016; Edger *et al.*, 2017; Wu *et al.*, 2018). Allopolyploidization occurs with homeolog expression variations in different phases. Parental legacy exerts an important effect on the immediate rewiring of homeolog expression after allopolyploidization, whereas evolution and domestication under allotetraploid continually promote homeolog-expression variations in reestablished sub-genome expression asymmetry (Wang *et al.*, 2016). In nascent allohexaploid wheat, considerable microRNAs exhibit nonadditive expression after polyploidization (Li *et al.*, 2014). In addition, these epigenetic changes include small RNA (Li *et al.*, 2014; Shen *et al.*, 2014; Jiao *et al.*, 2018), lncRNAs (Wang *et al.*, 2018; Wang *et al.*, 2020), DNA methylation (Chen and Chen, 2008; Xu *et al.*, 2009; Edger *et al.*, 2017) and histone modification (Song and Chen, 2015; Jiao *et al.*, 2018). Epigenetic variations alter the expression of around 20–50% mRNAs, providing a molecular basis for hybridization and polyploidization viability (Li *et al.*, 2014). In addition, alternative splicing variations constitute a key part of the transcriptome shock of novel allopolyploids (Zhou *et al.*, 2011; Yu *et al.*, 2020).

Investigating the mechanisms behind the survival of a newly formed allopolyploid will highlight the key roles of epigenetic regulation. Improved high-throughput methods, such as omics-aided assay of genomic and epigenomic approaches provide an opportunity to further understand the role of DNA methylation at a larger scale with greater resolution (Milosavljevic *et al.*, 2021). *De novo* genome assembly of newly synthesized allopolyploid and comprehensive comparative analysis provided a promising strategy to systematically reveal genomic and epigenomic changes associated with polyploid evolution (Jiang *et al.*, 2021; Yu *et al.*, 2021b). Hybridization, not genome duplication induced most genomic variations of nuclear and chloroplast genomes through sequencing individuals which defines a time series with fourteen generations of inbreeding. Moreover, post-polyploidy genomic changes mainly occurred in the first few generations, and then decreased (Yu *et al.*, 2021b). Furthermore, concerted genomic and epigenomic changes of resynthesized and natural *Arabidopsis suecica* allotetraploids suggested balanced genomic diversifications of allotetraploids occur with convergent and concerted variations of DNA methylation and gene expression of two subgenomes (Jiang *et al.*, 2021). The example of genomic and epigenomic reconciliation can serve as the basis to stabilize subgenomic structure and function and promote adaptation in polyploid evolution. The paradox of rapid genomic reshuffling and genomic stability can be solved using omics-aided assay of genomic and epigenomic changes in newly synthesized allopolyploids to explain our comprehension about polyploid genome evolution and to provide a basis for editing genes and modifying epigenetic landscapes in crop improvement (Figure 2).

IV. *De novo* improvement of newly synthesized allopolyploids using genome editing

Creating new crops characterized by resistance to drought, soil salinity, and insect damage with superior nutritional quality can be a challenge to traditional breeding because of the complicated and diffuse genetic basis of these traits. The strategy of resynthesizing allopolyploids could contribute to biotic and abiotic tolerances of wild and elite crop types. However, the method is difficult to implement because it simultaneously introduces under-domesticated and undesirable traits into new species. Latest advancements in CRISPR-informed gene editing technology like base editors or prime-editing, combined with a deeper insight into the genetic basis for domestication, open up prospects for producing new crops by manipulating domestication-related genes among wild relative species (Lemmon *et al.*, 2018; Zsogon *et al.*, 2018; Kwon *et al.*, 2020). This approach was successful in the *de novo* domestication in wild allotetraploid rice (Yu *et al.*, 2021a), representing the paradigm shift in developing natural genetic diversity in plants by introducing domestication- and improvement-associated traits to wild plants exhibiting special traits. The *de novo* domestication or improvement strategy enables the quick and concise transfer of wild relatives to crops by remaining numerous valuable resilience and nutritional traits in domestication and breeding (Fernie and Yang, 2019; Khan *et al.*, 2019; Gasparini *et al.*, 2021; Zhu and Zhu, 2021).

For example, new allopolyploid *Brassica* oilseed crops were created to combat climate change using combinations of varieties or sub-genomes to produce novel allohexaploid *Brassica* oilseed crops with the potential of inter-subgenomic heterosis. The generation of a novel allohexaploid *Brassica* with allele combinations may lead to superior crop improvement and resistance against biotic and abiotic stresses (Tian *et al.*, 2010; Gupta *et al.*, 2016; Kumari *et al.*, 2020). The nutritional value of *Brassica* seed meals can be

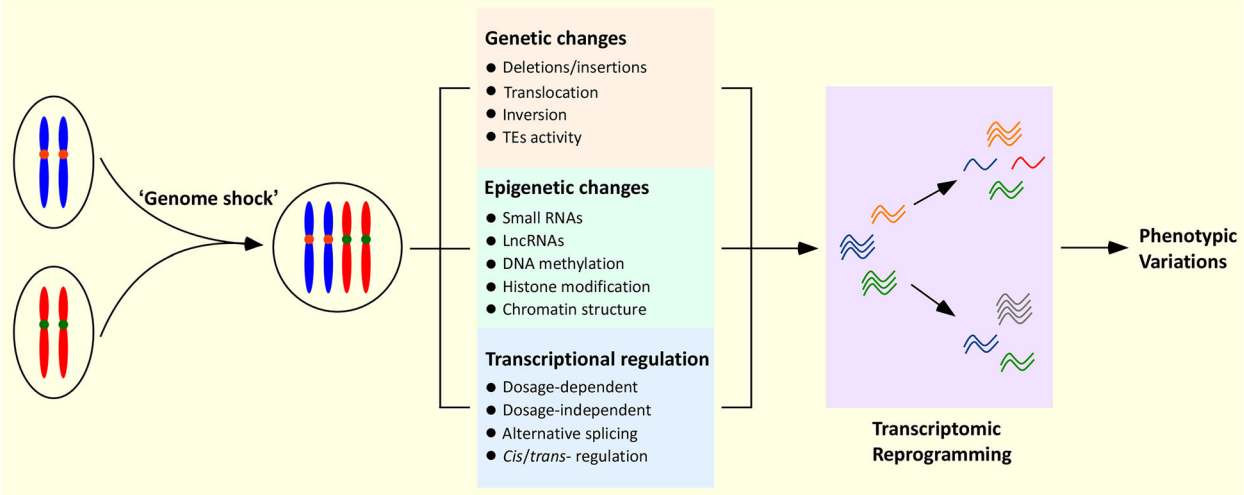

Figure 2. Summarized genetic and epigenetic regulatory mechanisms involving transcriptomic reprogramming in resynthesized allopolyploids. A bottleneck for allopolyploid formation is the postzygotic barrier which is associated with hybrid incompatibility and "genome shock" in newly synthesized allopolyploids. Genetic and epigenetic changes cause genome-wide transcriptomic reprogramming resulting in phenotypic variations in newly synthesized allopolyploids. The figure is derived from previous publications (Li et al., 2015; Song and Chen, 2015).

weakened due to glucosinolates, toxic compounds in plant defense of the *Brassicaceae* family (Halkier and Gershenzon, 2006). Most modern varieties with low glucosinolates content in seeds translate to a reduction in leaves (Li *et al.*, 1999) resulting in greater susceptibility to insect damage (Blau *et al.*, 1978), and diseases caused by plant pathogenic fungus *Sclerotinia sclerotiorum* (Fan *et al.*, 2008). Therefore, it is desirable to reduce glucosinolates content within seeds, yet maintain high levels in other organs (Lu *et al.*, 2014). Mutation of genes encoding two glucosinolates transporters (GTRs) could eliminate glucosinolates in *Arabidopsis thaliana*, *B. rapa*, and *B. juncea* seeds, but did not affect glucosinolates biosynthesis in leaves (Nour-Eldin *et al.*, 2012; Nour-Eldin *et al.*, 2017). Another risk of oil with high erucic acid, a straight-chained mono-unsaturated very-long-chain fatty acid, is that erucic acid can produce fibrosis of the myocardium and lowers the respiratory capacity of the heart mitochondria (Borg, 1975). The *fatty acid elongation 1 (FAE1)* gene had been identified a key gene that affects erucic acid synthesis in *Brassicaceae* (Kunst *et al.*, 1992; James *et al.*, 1995; Gupta *et al.*, 2004; Peng *et al.*, 2010; Kaur *et al.*, 2020). The new allohexaploid *Brassica* accumulates high levels of glucosinolates and erucic acid, depending on the selection of elite or wild relatives of inbred lines. Genome editing of these *GTRs* and *FAE1* enables the production of new allohexaploid *Brassica* with reduced seed glucosinolates and erucic acid content, presenting "double-low" quality of oil (Figure 3).

We consequently proposed a pipeline for the *de novo* improvement of newly synthesized allopolyploids required for crop improvement and future agriculture (Figure 4). These procedures include the following: (1) elite or wild relatives of inbred lines with specific traits are selected to synthesize allopolyploids via sexual or asexual hybridization (designed, synthesized allopolyploids); (2) omics-based approaches including genetics, genomics, transcriptomics, proteomics, metabolomics, and other techniques are used to identify causal genes associated with specific traits; (3) CRISPR gene editing methods are employed to generate mutations; (4) desirable traits, biotic and abiotic stresses tolerance, high yield, quality preferred, and other characteristics are combined and fixed to achieve new allopolyploids (*de novo* improvement of designed, synthesized allopolyploids).

V. Perspective

Plant breeding has delivered high-yielding crops over the past 100 years that have sustained human population growth. Climate change will increase abiotic stress, such as drought stress, heat stress, and biotic stress, such as insect and disease, resulting in much adverse condition for agricultural production. Developing next-generation crop varieties with modern breeding technologies can satisfy the needs of population growth in future decades. Creating new allopolyploids provides an index of useful traits present in each species that may be exploited.

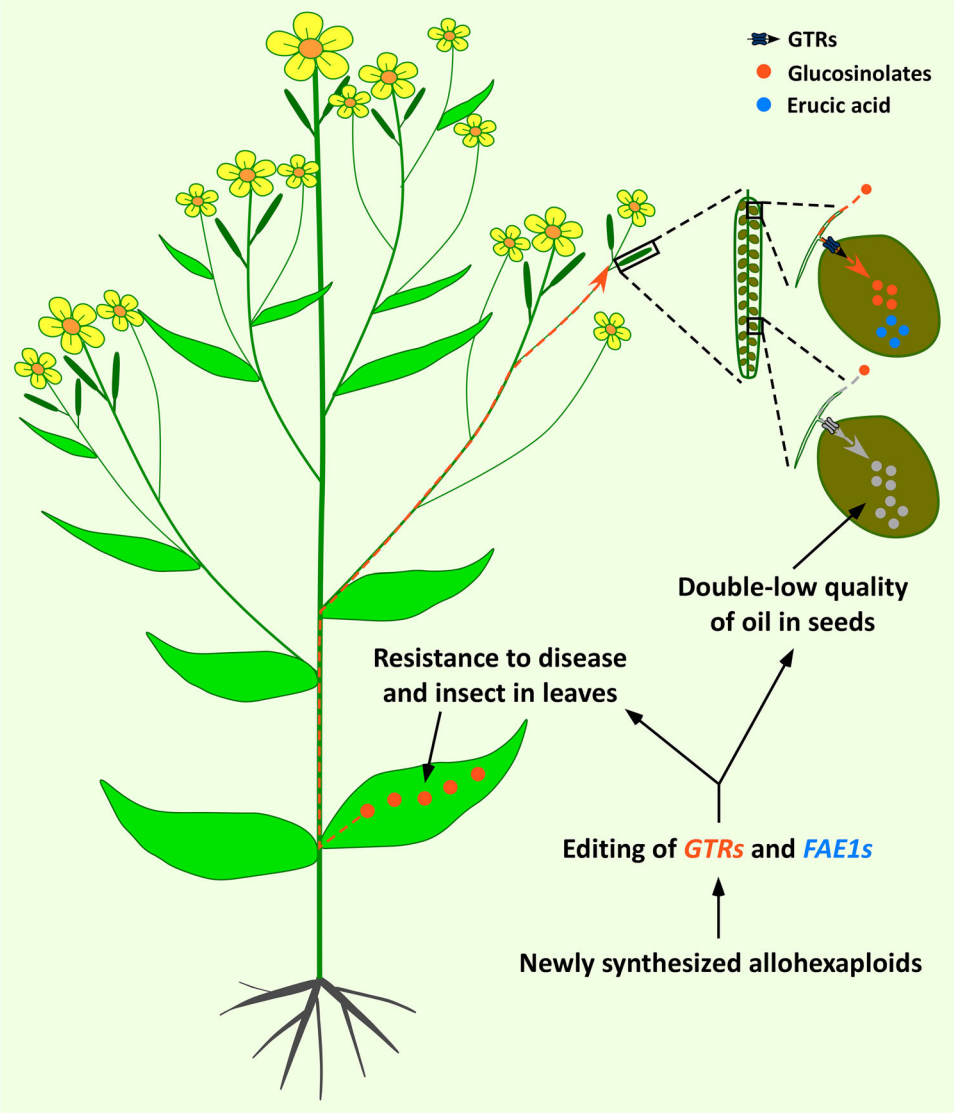

Figure 3. Development of double-low quality oil and resilience of new *Brassica* allohexaploid. Glucosinolates (orange dots) are mainly synthesized in leaves and transported into seeds by transporters and erucic acids (blue dots) are synthesized in seeds. Gray dots mean that glucosinolates cannot be transported into seeds or erucic acids cannot be synthesized in seeds. *GTRs*: glucosinolates transports; *FAE1*: fatty acid elongase 1.

Despite huge difficulties in utilizing wild relatives for crop improvement, the approach provides unexplored potential for crop improvement and crop resilience before global climate change.

Polyploidization provides niches for strict genome modification at the cytogenetic, genetic, and epigenetic levels. Studying the mechanisms conferring genomic stability is crucial to generate and construct a stable allopolyploid crop, and to offer reference to polyploid genome evolution. Comprehensive comparative omics-based analyses of new allopolyploid and their progenitors keep promoting the study of the processes as well as genetic and epigenetic consequences of polyploidy and interspecific hybridization, particularly in high accurate single-molecule long sequencing reads.

The experimental reproduction of wild species domestication is challenging and unfinished. According to numerous cases of independent crop domestication, the idea was reasonable, though many domestication cases were mostly promoted by gene flow in cultivated populations. *De novo* domestication for a new wild species is more difficult because of the complicated genetic basis of domestication traits, limitations in life history, and long time required (Stetter *et al.*, 2017). Marker-assisted selection allows this process to avoid the loss of edited alleles or genomic changes in a larger newly synthesized allopolyploid

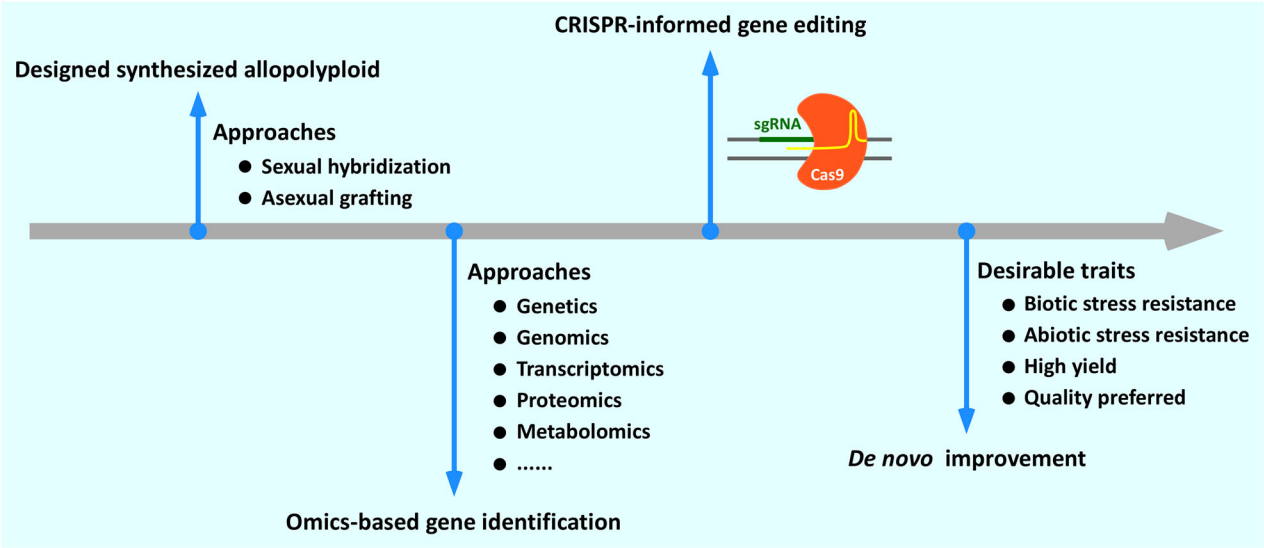

Figure 4. *De novo* improvement of designed and synthesized allopolyploid. Approaches include (1) parent lines with specific traits are selected to newly synthesize allopolyploids called designed synthesized allopolyploids; (2) omics-based approaches identify causal genes associated with specific traits; (3) CRISPR-informed gene editing methods generate mutations; and (4) desirable traits are combined and fixed to achieve new allopolyploids.

population. Meanwhile, other double haploid induction, high-throughput phenotyping, and speed breeding can shorten the breeding process.

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Disclosure statement

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